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# BIOLOGICAL BULLETIN

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## SPERM-TRANSFER ORGANS IN CAMBAROIDES.

E. A. ANDREWS.

Amongst the arthropods it is not uncommon for some of the limbs to be used for transferring the sperm from the male to the female. In some of these cases the path of the sperm from the male to the egg is very complex, and we may speak of "indirect sperm-transfer."

Thus in the common crayfishes of the United States, of the genus *Cambarus*, the first and the second limbs of the abdomen of the male are special organs that we will call the first and the second stylets, which conduct the sperm from the male openings upon the bases of the fifth pair of walking legs to the surface of the female. In the female the sperm is received into a pouch in the shell on the under side, between the fourth pair of walking legs. This sperm receptacle is hollowed out in the so-called annulus, or special sternal plate, and in this pouch the sperm remains till the eggs are laid. In the crayfish of Europe, however, the sperm conveyed by the stylets is deposited freely over the sternum, in secreted tubules, or spermatophores, and there is no sperm receptacle.

There are then two forms of indirect sperm transfer within this family, in the two genera *Cambarus* and *Astacus*.

The crayfish of Japan and the Amoor River region are so different from other species of *Astacus* that it is a question whether they do not form a distinct genus. They resemble *Cambarus* so much that Faxon called them *Cambaroides*. Nothing is known as to the method of sperm transfer in this *Cambaroides* subgroup of *Astacus*, but the following account of the anatomy of the organs concerned may aid in a tentative view as to what actual observation of the process may reveal.

The material used was kindly loaned by the National Museum,

and consisted of a very few specimens of *Astacus* (*Cambaroides*) *similis* from Corea and some ten specimens of *Astacus* (*Cambaroides*) *japonicus* from Hakodate, Japan. These last were obtained by the "Albatross" from the market in July, 1906, and were remarkable in being all strung along upon bits of stick that had been thrust through several crayfish, one after the other, passing through the head-thorax and abdomen lengthwise. From the condition of internal anatomy the specimens would appear to have been dried before they were preserved by the naturalist.

Observations upon *Cambarus* have shown that when the stylets are being used to fill the sperm receptacle the male is firmly fastened to the female by two pairs of hooks, or spines, that stand out like spurs from the walking legs and are carefully fitted into the groove between the segments of the legs of the female. In fact, experiments show that without these spines the

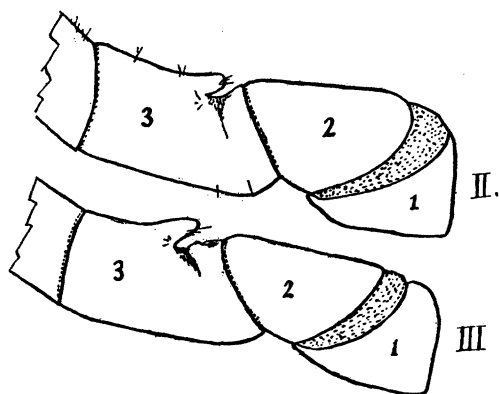


FIG. 1.

other organs are of no avail as the male is not able to transfer the sperm to the sperm pouch. In *Cambarus* there are then three sets of necessary external organs concerned in sperm transfer, the hooks and the stylets of the males and the sperm receptacles of the females.

In *Cambaroides* the hooks are present as well as the stylets but in the females there is no discovered receptacle though the annular plate is somewhat modified.

We will describe these three sets of organs, in the following order: hooks, stylets, annular plate of female.

In *Cambaroides similis*, a specimen 55 mm. long had the hooks developed as in Fig. 1, a blunt rounded spine upon the third segment of the second and the third walking legs. Each spine

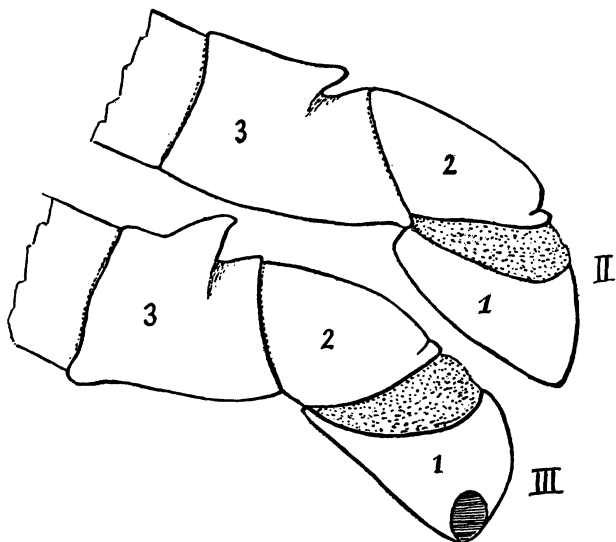


FIG. 2.

bears a few setæ. They are like the spines of *Cambarus Montezumæ* in being on the second and third legs, but are much shorter, more blunt and less effective as hooks. The spine of the third leg is the better developed.

In *Cambaroides Japonicus*, Fig. 2, the hooks are essentially the same, but more pointed. In both cases the resemblance of the hooks to those used by *Cambarus* is so strong that one would infer that they are probably functional in *Cambaroides*.

In comparing the stylets of *Cambaroides* with those of *Cambarus* we note that the first lacks the fine detail of apex commonly found in *Cambarus* and is a more stout and undifferentiated organ. In *Cambaroides similis*, Fig. 3, the first stylet is a clumsy cylinder having a movable joint between the long protopodite and the somewhat longer distal endopodite.

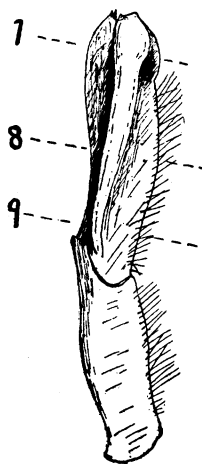


FIG. 3.

Both bear a fringe of setæ along the external edge. This long line of setæ seems to represent what is found upon the edges of the common pleopods and may be regarded as a mark of little specialization or of retention of primitive characters, since in *Cambarus* it is generally specialized as a local group of setæ, or at most in *C. Clarkii*, as a less simple line.

The main features of the endopodite are, however, a shallow groove and a very stout ridge along the posterior face, external to the groove. This ridge ends distally as a swelling that is part of the specialized tip of the organ. More enlarged, Fig. 4,

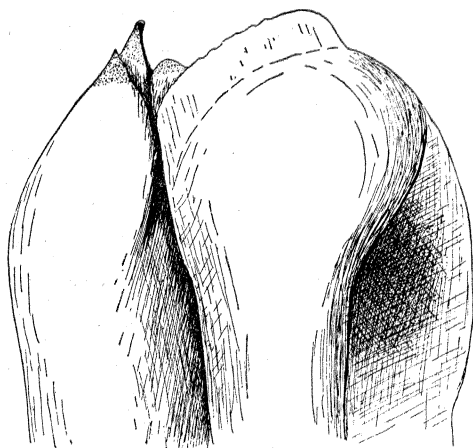


FIG. 4.

the tip shows the rounded head in which the ridge ends, the groove to the left of it and a depression to the right. The actual ending of the organ is a sort of complex edge, flattened from before back.

On the median side of the groove are two horny points, the shorter posterior, the longer anterior. The posterior is comparable to the large "spatula" and the anterior to the large "canula" of *Cambarus Montezumæ*. External to the groove is a short, blunt anterior point, comparable to the "ligula" of *C. Montezumæ* and a long thin knife edge that is a continuation of the rounded head of the ridge. The organ appears fitted to open a slit into which sperm might flow from the groove.

In *C. Japonicus* the two first stylets lie side by side with diver-

gent tips. In a male 45 mm. long, with stylets 8 mm. long, their tips were two millimeters apart, across the median line. Each stylet has the same structure as in *C. similis*, with only slight differences in proportion, but the groove opens more toward the median face and is not seen from behind, Fig. 5. While the tip Fig. 6 presents the same details as in *C. similis*, Fig. 4, the cutting edge is less sharply set off from the head of

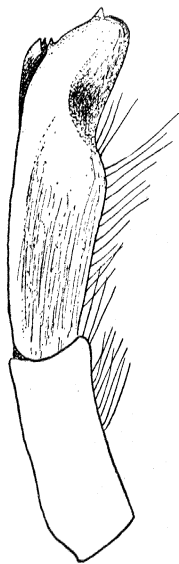


FIG. 5.



FIG. 6.

the ridge and runs out externally as a pronounced angle or spine, that is lacking in the former species.

From an end view the tip of the organ of *C. Japonicus* is complexly modelled and suggest not a cutting tool but a probe to be forcefully inserted against resistance.

Serial sections of the first stylets of both species show the same inside structure. A thick, firm shell covers the soft

areolar tissue and a delicate epidermis underlies the shell and is continuous with the areolar tissue. The internal anatomy and the external modelling is shown by the series of sections, Figs. 7, 8, 9, cut along the lines 7, 8, 9 of Fig. 3. The organ is essentially a thick, flat plate with a groove on its posterior face dividing it into a smaller median part that we will call the median mass and a larger external mass, *M.M.* and *Ex.m.* in Fig. 7.

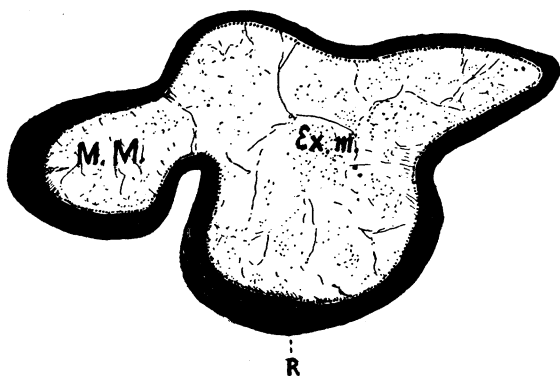


FIG. 7.

The groove is made much deeper by the fact that a great ridge, *R*, rises up from the external mass and forms the external boundary of the groove. In the middle of the course of the groove the ridge, Fig. 8, extends toward the middle line of the

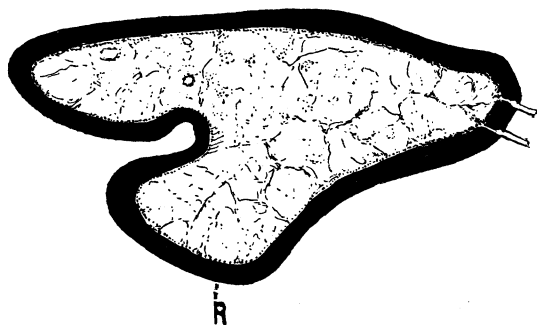


FIG. 8.

body parallel to the median mass so that the groove is here deep and narrow and opens out more to the median face of the organ. Toward the basal end, Fig. 9, the shallow groove is bounded by

the diminishing terminal part of the ridge. At this level also may be seen the muscle mass that extends into the endopodite and indicates that the joint between the endopodite and exopodite may actually be used and the position of the tip of the organ be

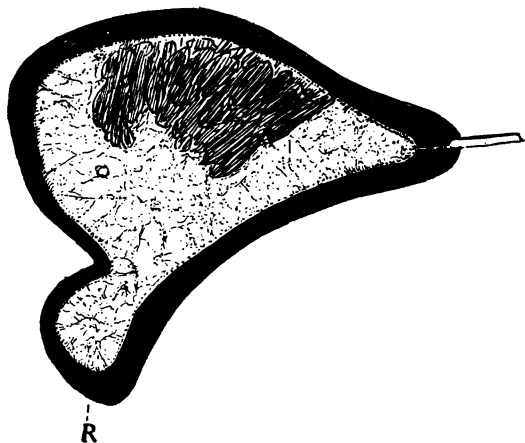


FIG. 9.

directed by this muscle. This muscle was also seen in cleared mounts in toto.

In the same manner in *C. Japonicus* sections show only a simple groove and large ridge, with the only difference that the groove faces more toward the median aspect of the organ, so that the above Figs. 7, 8 and 9 would well represent the condition in both species.

The second stylet preserves the usual pleopod form in that it is forked, or has both endopodite and exopodite. In *Astacus* (*Cambaroides*) *Japonicus*, Fig. 10, the exopodite is a slender obscurely segmented filament bearing few long setæ while the endopodite is the wide massive terminal part of the stylet. The tip of this endopodite, the flabellum, bears a long tuft of setæ and is evidently like the tip of the exopodite, but much enlarged. In the median edge of the endopodite there arises the extra element comparable to the "triangle" of *Cambarus*, that probably has some use in sperm transfer. This is a thick ridge that rises up as a free, thumb-like process directed diagonally across the endopodite. It has a marked angular elbow on the median side



and terminates in an oblique and somewhat hollowed face posterior to the flabellum. This very simple representative of the triangle of *Cambarus* and the scroll of the American and European *Astacus*, bears still a few setæ, several upon the median and two or three upon the external border. In this it is intermediate between the above two crayfish.

The entire appendage seems crude and clumsy, either primitive or reduced.

This appears again in the other species of *Cambaroides*, *C.*

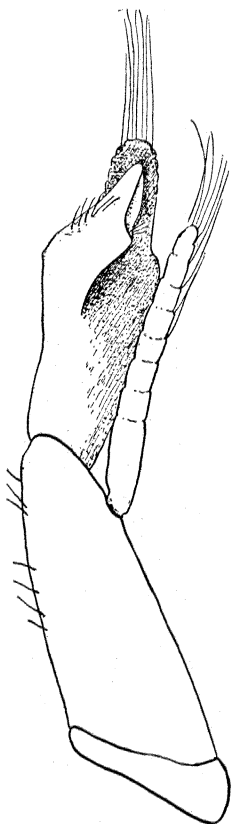


FIG. 10.

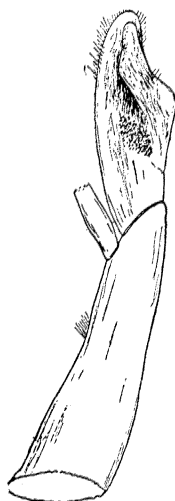


FIG. 11.

*similis*, Fig. 11, which is like *Japonicus* but the setæ are very short and the flabellum more reduced. The dotted area in Fig. 11 is membranous. The posterior face is turned so that the

triangle can fit into the groove in the first stylet. In *Cambarus* the projection of the second stylet fits accurately to the groove of the first stylet and insures sperm transfer and in *Cambaroides* we can see that the projection upon the second will run in the groove of the first but it does not seem nicely adjusted to it.

Another departure from the finer adjustments of *Cambarus* may be inferred from the simpler mode of ending of the defferent duct. While in *Cambarus* it ends in a soft papilla that is fitted

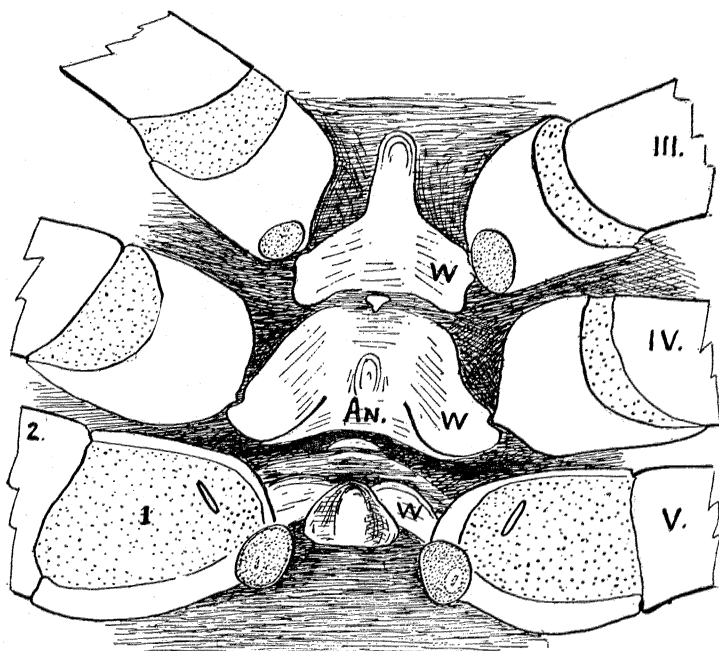


FIG. 12.

into the groove of the first stylet, in *Cambaroides* there is, at least in the preserved specimens, only a rounded, slightly raised area with a slit in it for the exit of the sperm.

The under side of the thorax of the male, Fig. 12, shows the ending of the defferent duct as a small opening in a rounded raised area on the base of the fifth leg, right and left. In *Cambaroides japonicus*, Fig. 12, these rounded areas are soft and the entire adjacent surface of the base of the leg is also membranous, as indicated by the dotted region, except for the minute hard

oblique ridge isolated in the membranous area. In *Cambaroides similis*, the base of the fifth leg shows a large white area thought to be glandular, the area 1 in Fig. 13, and the ending of the deferent duct is in a solid projection with a slit-like orifice.

Whether in life a soft papilla can be projected from these

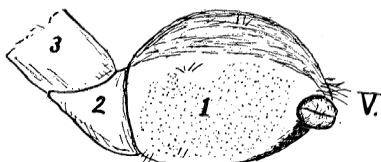


FIG. 13.

orifices is doubtful, but the hard and slightly projecting areas can be put against the groove in the first stylet in such a way that we infer the sperm may be poured out into the groove of the stylet, with perhaps some aid from the second stylet.

Turning now to the destination of the sperm transferred by the

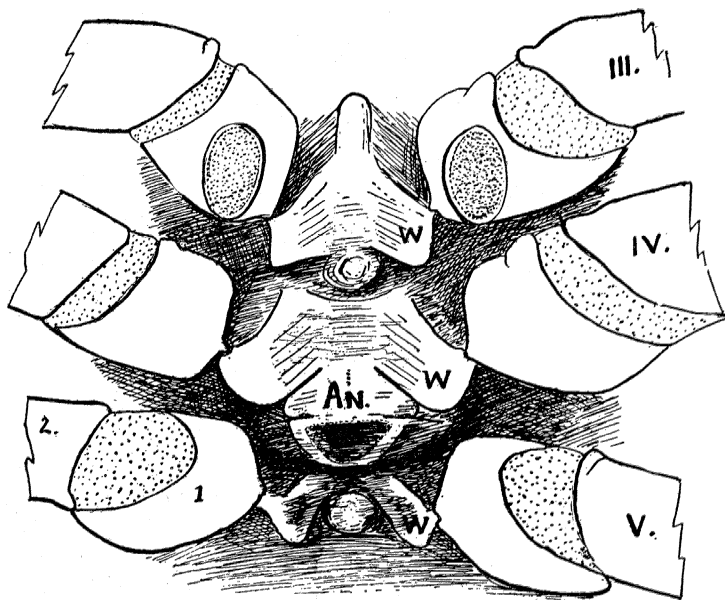


FIG. 14.

above male organs we fail to find upon the female any specialized receptacle. The under side of the thorax of the female *Cambaroides Japonicus*, Fig. 14, has a series of median plates between

the limbs *III*, *IV* and *V*. Each plate expands toward the limbs as a lateral wing, *W*, each plate is also modified in its central part. Between the third limbs the central part shows a rounded boss and an anterior prolongation; between the fifth limbs there is only a boss; between the fourth limbs the median part of the plate is prolonged backward not as a boss but as a large expanse, the annular plate, *An*. This annular plate is subdivided into an anterior part, *An*, somewhat convex from side to side and a posterior part which is hollowed out as is poorly shown in Fig. 14.

The hollowed posterior part of the annular plate rises up dorsally at an angle with the horizontal anterior part.

The median depression is quite shallow and neither in surface views nor in sections is there any slit or internal pocket such as is characteristic of the annular plate of the genus *Cambarus*. Thus while in both *Cambarus* and *Cambaroides* there is an annular plate only in *Cambarus* is it provided with an internal cavity. It is the internal cavity in the annular plate that is filled with sperm. In these specimens of *Cambaroides* no sperm pocket is found.

In the male *Cambaroides*, Fig. 12, there is also an annular plate between the fourth limbs but it lacks the hollowed posterior part that is found in the female.<sup>1</sup>

In a specimen of *Cambaroides similis* the posterior part of the annular plate is less sharply hollowed out than in *C. Japonicus*.

The use of these various male and female parts can, as yet, only be inferred from comparisons with the organs of *Astacus* and of *Cambarus* whose use has been observed. But in applying the male to the female we are led to imagine that the stylets may deposit spermatophores between the fourth and fifth limbs.

<sup>1</sup> In the individual male figured here there is an abnormal pair of structures that simulate the openings of oviducts. In the female the oviduct openings, Fig. 14, are large elliptical membranous areas upon the bases of the third limbs. In the male the openings of the deferent ducts are more elevated areas upon the bases of the fifth limbs, Fig. 13. There is thus both a difference in position and in character between the male and the female openings. The abnormal openings upon the third legs of the male figured in 12, are like female openings both in position and character though they are smaller than normal and the one upon the right of the animal is especially small (see also Fig. 2). This then seems to be a case of partial mixture of sex organs such as have been described in both *Astacus* and *Cambarus* (see *Am. Nat.*, 1909).

On the whole the sex organs of *Cambaroides* are more like those of *Cambarus* than like those of *Astacus*. That is, the hooks are present in *Cambarus* and *Cambaroides*, but not in *Astacus*. From their form we may infer that in *Cambaroides* they are used to hold the female just as they are used in *Cambarus*. The stylets in *Cambaroides* lack the flat scroll form of *Astacus* and are more like the stout complexly tipped organs of *Cambarus*, but they are much more simple. They doubtless serve to transfer the sperm as in both *Astacus* and *Cambarus*. In the female the annular plate of *Cambaroides* lacks the special sperm reservoir of *Cambarus* and is thus like *Astacus*, but it is more developed and somewhat hollowed out. In this respect it recalls the earliest phase of the ontogeny of the annulus of *Cambarus*.<sup>1</sup>

In brief the organs of *Cambaroides* are more simple than those of *Cambarus* but fashioned somewhat like them, suggesting some connection closer with *Cambarus* than with *Astacus*.

How are these facts to be interpreted? The general anatomy shows that *Cambarus* is the recent and *Astacus* the more unspecialized genus. Is *Cambaroides* a step from *Astacus* toward *Cambarus* or is it a step backward from *Cambarus*?

Since *Cambaroides* has the same gill formula as *Astacus* and is like *Astacus* in having no sperm receptacle (as far as known), while on the other hand it has hooks like *Cambarus* and stylets similar to those of *Cambarus*, we may regard it as a genus separate from both *Astacus* and *Cambarus*.

It then becomes a question of the relative positions of these three genera. Granting that the larger number of gills is primitive and the small number derived we must assume either that the presence of hooks in *Cambarus* with few gills and in *Cambaroides* with more gills is a case of secondary convergence from parallel variation or else that it is a common inheritance. Ortman has assumed the resemblances of *Cambarus* and *Cambaroides* due to convergence, but Faxon regarded them of more significance. The new facts as to the annular plate and the structure of the stylets will aid in the solution of this question; with emphasis upon the sex organs as criteria of relationship, which has been the tendency of all recent work upon this group.

As elsewhere shown<sup>1</sup> some of the Penæidæ as well as the lobsters have sperm receptacles whence we may infer that a sperm receptacle was common to the ancestors of the crayfish. In such case the absence of sperm receptacle in *Astacus* would be due to loss, and the presence in *Cambarus* to retention of the ancestral mode of sperm transfer. If we suppose that the resemblances and differences of organisms are connected with chance variations it seems more likely that organs may have been independently lost, in separate animals, than that the same organ should have been independently acquired in separate organisms. We would then say that *Cambaroides* and *Cambarus* are closely related as both have retained the hooks and the general form of stylets of some ancestor but that *Astacus* and *Cambaroides* are not so closely related though both have independently lost the sperm receptacle while changing the form of stylets.

Adopting Ortmann's views as to the origin of the present distribution of crayfish we would modify it chiefly by the assumption of two migrations from Asia into America. We would think of ancestral Asiatic crayfish with many gills and a sperm receptacle of some sort filled by some use of the abdominal limbs. One set of descendants retaining more gills but losing the sperm receptacle became the *Astacus* of America and Europe as well as the crayfish of the southern hemisphere. While another set of descendants became *Cambarus* and *Cambaroides*. Part of this branch migrated into America and ultimately, in Mexico according to Ortmann's evidence, became the present *Cambarus* with reduced gills and highly specialized receptacle and stylets. The other part remaining in Asia independently lost the receptacle but retained the larger number of gills as well as the hooks.

We might then find in *Cambaroides* indications of the former presence of a sperm receptacle. As such we regard the hooks that have no known use except as aids for the filling of a receptacle. As such we regard the presence of ligula, spatula and canula at the tip of the stylet.

The absence of a tubule in the stylet, its clumsy form and the reduced prominence of its tip as well as the simplicity of the triangle of the second stylet might also be regarded as signs of degeneration.

But speculation is here very insecure and if use inheritance or some law of perfection were known it would be easy to argue that *Cambaroides* was an incipient *Cambarus* evolving from *Astacus*. In any case the common ancestor of *Cambarus* and *Cambaroides* must have been far back as it had the larger number of gills and as *Cambaroides* has the primitive characters of a well-developed flagellum on the first stylet and a muscle at the movable joint between protopodite and endopodite.

A diagram of the three genera would place *Astacus* and *Cambaroides* near together as having the same gill formula and as lacking a sperm receptacle, while *Cambarus* should stand apart as having a simplified gill formula and also very highly developed sperm-transfer organs, including a sperm receptacle. At the same time the diagram should indicate that *Cambarus* and *Cambaroides* kept together after departing from *Astacus*, and that later *Cambaroides* went off in the direction of *Astacus*, leaving *Cambarus* as at once the most specialized in its gills and the most conservative in its retention of the very ancient crustacean mode of sperm transfer by the employment of a sperm receptacle.

BALTIMORE, June 10, 1909.